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Naso-temporal asymmetry of the N170 for processing faces in normal viewers but not in developmental prosopagnosia

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Abstract

Some elementary aspects of faces can be processed before cortical maturation or after lesion of primary visual cortex. Recent findings suggesting a role of an evolutionary ancient visual system in face processing have exploited the relative advantage of the temporal hemifield (nasal hemiretina). Here, we investigated whether under some circumstances face processing also shows a temporal hemifield advantage. We measured the face sensitive N170 to laterally presented faces viewed passively under monocular conditions and compared face recognition in the temporal and nasal hemiretina. A N170 response for upright faces was observed which was larger for projections to the nasal hemiretina/temporal hemifields. This pattern was not observed in a developmental prosopagnosic. These results point to the importance of the early stages of face processing for normal face recognition abilities and suggest a potentially important factor in the origins of developmental prosopagnosia.

Keywords: N170; Prosopagnosia; Naso-temporal asymmetry; Non-LGN based vision; Subcortical visual processing

Research on human visual abilities through normal lifespan and in brain damage draws attention to visual abilities of the brain that are not based on pathways critically involving latero-geniculate nucleus (LGN). Findings of several studies [9,11,13,17] suggest a role of an evolutionary ancient visual system based on the retinotectal pathway, which plays a role not so much in object recognition but in early detection and subsequent visually guided behaviour. Evidence for involvement of this alternative visual route has been obtained by taking advantage of a putative property of the visual system, the asymmetry between projections from the nasal and the temporal hemiretina [3,6,15,19,23]. This asymmetry is related to the fact that the temporal visual field projecting to the nasal hemiretina is more dominantly represented due to crossed fibres connecting the nasal retina to the superior colliculus (and possibly to other brain centres).

The functional meaning of the nasal retina advantage has been illustrated in infant research on face recognition [22]. Bronson [4] proposed the theory that cortical activity takes over from subcortical processes during early development. Johnson and co-workers elaborated on this notion and proposed an influential model of the development of face recognition [10,18]. The ontogenetically early face system (CONSPEC) is presumably tuned to orient newborns to face-like stimuli. The cortical face processing system (CONLERN), which develops after the initial face sensitivity, continues to evolve well into childhood and ultimately supports the sophisticated face identification abilities of normal adults.

Evidence for visual abilities not based on LGN-cortical pathways has also been obtained in a very different population, patients with hemineglect [21] and patients with complete unilateral lesion of striate cortex who show residual vision [24]. The latter group of patients can reliably discriminate facial expressions shown to them in the blind field [9]. Moreover, results from brain imaging indicated that superior colliculus and pulvinar play a critical role [17] indicating that

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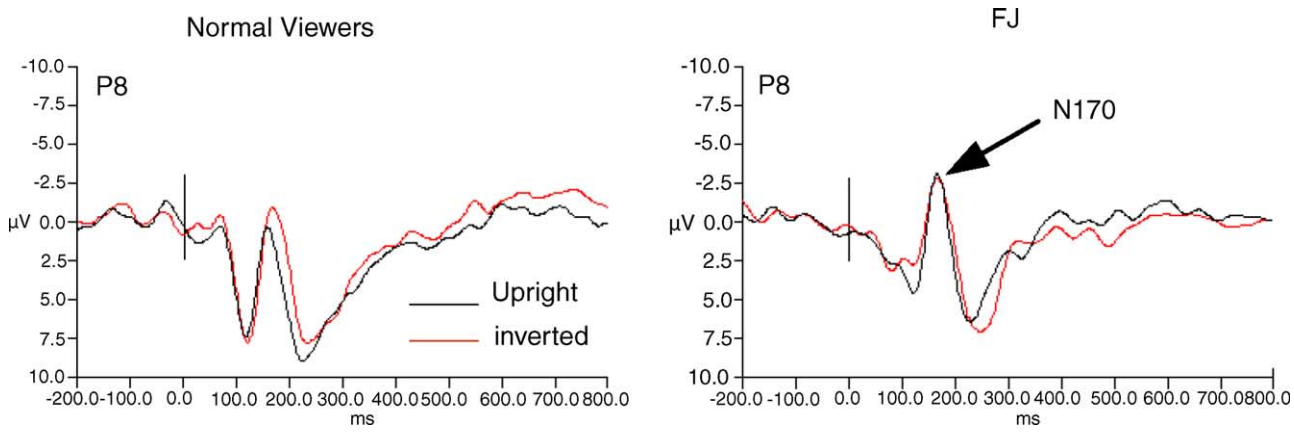

Fig. 1. ERPs of normal viewers and F.J. at electrode position P8 evoked by central presentation of upright and inverted faces.

an extra-LGN pathway is active in patients who sustained striate cortex damage as a child or in adulthood. Thus, a non-LGN based pathway including subcortical structures for face processing remained functional even after the LGN-based cortical pathways are fully developed. This in turn raises the possibility that a non-dominant subcortical route exists also in normal adults and could sustain a restricted number of visual functions. The possibility of a temporal hemifield advantage for face processing in normal adults has not been explored systematically as the majority of studies used normal adults and face stimuli in foveal vision, thereby tapping mostly higher visual processes.

At present no direct non-invasive methods are available for exploring this issue in humans. However, measuring event-related brain potentials (ERPs) from the scalp is a very useful method for investigating the time course of face processing in the brain even if the putative source of a face related potential like the N170 [1] is rather deep in fusiform cortex. Measuring ERPs to faces does not provide a direct window on subcortical processes but it allows inferences about the early stages of face processing and about selective involvement of the nasal versus the temporal hemifields. The N170 to face stimuli is highly sensitive to face orientation (and picture-plane orientation in particular) as indicated by the fact that inverted faces elicit a delayed and higher amplitude N170 component than upright (normal) faces [14]. The N170 appears to reflect the earliest stages of face processing related to the encoding of faces and is unaffected by semantic factors due for example to face familiarity [5,14].

Our goal was to test whether the face sensitive N170 could also be observed with peripheral face stimuli and whether with monocular vision side of presentation in either the nasal or the temporal hemiretina would modulate the N170. We recorded ERPs for faces presented in the periphery under monocular viewing conditions. Subjects performed a task at central fixation which was entirely unrelated to the stimuli shown in the periphery. With this procedure the N170 would reflect unattended face processing and automatic covert orientation to faces. We used photographic quality pictures instead of the schematic faces used in developmental studies because sensitivity for schematic face patterns is lost after a few weeks [23]. Besides a group of normal participants we tested a subject with developmental prosopagnosia. We predicted that his face recognition deficit may be reflected in the absence of a face inversion effect on the N170. Moreover, we predicted that he would not show a nasal hemiretina advantage of the N170 to upright faces, a finding that may provide important indications about possible causes of developmental prosopagnosia.

We tested 11 healthy right-handed viewers and a 40-year-old male developmental prosopagnosic (F.J.) [7]. The experiments were conducted in accordance with the Declaration of Helsinki. All procedures were carried out with the adequate understanding and written consent of the participants. F.J. was presented with clinical neuropsychological tests and in a separate study we investigated his visual skills and his object and face recognition abilities. F.J. is unable to recognize individual faces as indicated by a score of 28/52 on the Benton Face Recognition, but has no visual problems as indicated by a normal score on object recognition subtests of the Birmingham Object Recognition Battery (BORB) and on the Boston naming test (score 58/60). He is unable to tell apart famous faces from unknown ones. Speeded categorisation of faces (score of 36/36) and objects (35/36) is at ceiling like that of normal controls except for response latency. Face identity recognition tests indicate that F.J. does not rely on configural processes to tell individual faces apart. On experimental tasks investigating the inversion effect his behavioural pattern is similar on these tests (i.e., similar performance for inverted faces compared to upright faces) to that obtained previously with another developmental prosopagnosic [16]. F.J. also showed no face inversion effect at the electrophysiological level (Fig. 1), which is consistent with an earlier study on face processing in a prosopagnosic [12].

Materials consisted of five greyscale frontal photographs of male faces subtending a visual angle of 6.9° by 9.1° at 50 cm viewing distance. Pictures were used in previous studies with normal viewers and prosopagnosics [7]. The ex-

periment comprised two blocks with central presentations in binocular vision and eight blocks with hemifield presentations in monocular vision (four blocks with the left eye blinded with an eye patch and four blocks with the right eye blinded). The blocks with central presentations were conducted to examine whether F.J. showed a face inversion effect at the electrophysiological level and contained 30 upright and 30 inverted faces that were presented randomly. The blocks with hemifield presentations comprised 30 trials (5 stimuli × 2 positions × 3 repetitions), 25 required passive viewing and 5 were foils, during which participants performed a task assigned to the central fixation. With the left eye blinded, a face stimulus falling in the left visual field was viewed by the temporal part of the retina of the right eye. With the right eye blinded, the stimulus was viewed by the nasal part of the retina of the left eye and the reverse situation holds for a stimulus presented in the right visual field. Patient F.J. was tested in two separate sessions on two consecutive days. Blocks were exactly the same as with normal participants but were repeated 18 times in order to increase the signal to noise ratio. A trial started with presentation of a central cross for 200 ms, which was either white (83.3%) or grey (16.7%) followed by a homogenous dark screen presented for 300 ms and then by the stimulus (presented either centrally or peripherally) for 150 ms and a dark screen (750 ms), used as constant inter-trial interval. For hemifield presentations, horizontal separation between the central cross and the outer edge of the face was 8.0°. An active oddball design was used in which participants were instructed to monitor whether the fixation cross was either white (standard) or grey (deviant). Deviant trials (16.7%) required participants to respond by pushing a button and were not analysed.

EEG was recorded from 64 electrodes (Neuroscan), mounted in a Quickcap (10–20 System) with a linked-earlobes reference. Eye movements were monitored (EOG) with bipolar electrodes affixed above and below the left eye as well as at the outer canthi of both eyes. EEG signals were band-pass filtered (0.01–30 Hz) at a sample rate of 500 Hz and off-line referenced to an averaged reference. The raw data were segmented into epochs of 1000 ms, including a 200-ms prestimulus baseline. Epochs with an amplitude change exceeding ±70 μV at any EEG or EOG channel were automatically rejected. Waveforms were averaged separately for all conditions (upright and inverted faces for central presentations and upright faces for the four hemifield presentations in monocular vision). Statistical analyses were performed on the amplitude and latency parameters of the N170 component for the experimental trials (83.3% of the total number of trials) during which passive viewing was required. The N170 was defined as the most negative peak between 120 and 240 ms relative to pre-stimulus baseline. Three participants were not included in the analyses because of excessive alpha band contaminating the visual ERPs.

Behavioural results indicate that performance on the monitoring task was near ceiling, that is, above 97% of correct irrespective of condition with less than 0.3% of false alarms. Similarly, patient F.J. performed above 98% correct, missing less than 0.5% of the targets.

We first present electrophysiological data for central presentations with binocular vision (Fig. 1). Eight electrode sites P7/8, P5/6, PO7/8, and PO5/6 were selected a priori for statistical analyses based on previous electrophysiological studies focused on face perception. With central presentations and binocular vision, normal viewers had a clear N170 component for upright faces. Peak N170 latency and amplitude were tested using a multivariate analysis of variance for repeated measures with Orientation (upright, inverted), Hemisphere (left, right), Anteriority (P7-P5-P8-P6 line, PO7-PO5-PO8-PO6 line) and Electrode Site (P7/P5, PO7/PO5, P8/P6, PO8/PO6) as factors. Inverted faces elicited a delayed and larger N170 than upright faces in both hemispheres whatever the preselected electrode site considered, $F(1, 7) = 13.79$, $p < 0.01$, $F(1, 7) = 10.7$, $p < 0.05$, respectively. In F.J., centrally presented upright and inverted faces elicited a clear-cut N170 component in both hemispheres, which did not vary in amplitude and latency with face orientation.

For monocular presentations, our research goal was to assess whether the N170 could be modulated by the naso-temporal manipulation. We first present the data for left visual field (LVF) presentations with monocular vision (Fig. 2). In normal viewers, we found that faces presented at the nasal part of the retina elicited a higher N170 compared to faces presented at the temporal part. This effect depended on the interaction between Hemisphere and Electrode position, $F(1, 7) = 9.46$, $p < 0.05$, The strongest effects of the nasal hemiretina advantage were found in the right hemisphere for both lateral electrodes, $t(7) = 3.54$, $p < 0.01$, and medial electrodes, $t(7) = 3.72$, $p < 0.01$. For F.J., the N170 was highly reduced in the left visual field condition and was not affected by the naso-temporal manipulation in the left hemisphere. Unlike what is observed in normal viewers, no nasal hemiretina advantage of N170 amplitude was found in the right hemisphere of F.J.

In the right visual field (RVF) condition, N170 amplitude for normal viewers was higher for temporal than for nasal projections, in the right hemisphere (for lateral electrodes, $t(7) = 10.99$, $p < 0.001$; for medial electrodes, $t(7) = 5.7$, $p < 0.001$). The reverse pattern was found for F.J. In the right hemisphere, the nasal hemiretina N170 was higher than the temporal hemiretina N170.

Our major result is that normal viewers have a higher sensitivity to faces in the nasal hemiretina. This pattern was not observed in the prosopagnosic subject. The absence of this signature effect points to a possible relation between developmental face deficits and normal development of subcortical and cortical face processes. Our results also provide clear evidence that a N170 can be obtained for unattended faces presented in the periphery and under monocular viewing conditions, an observation not reported previously.

The central contribution of our study concerns the modulation of the amplitude of the N170 by retinal hemifield. In line with our predictions, monocular presentations generate a

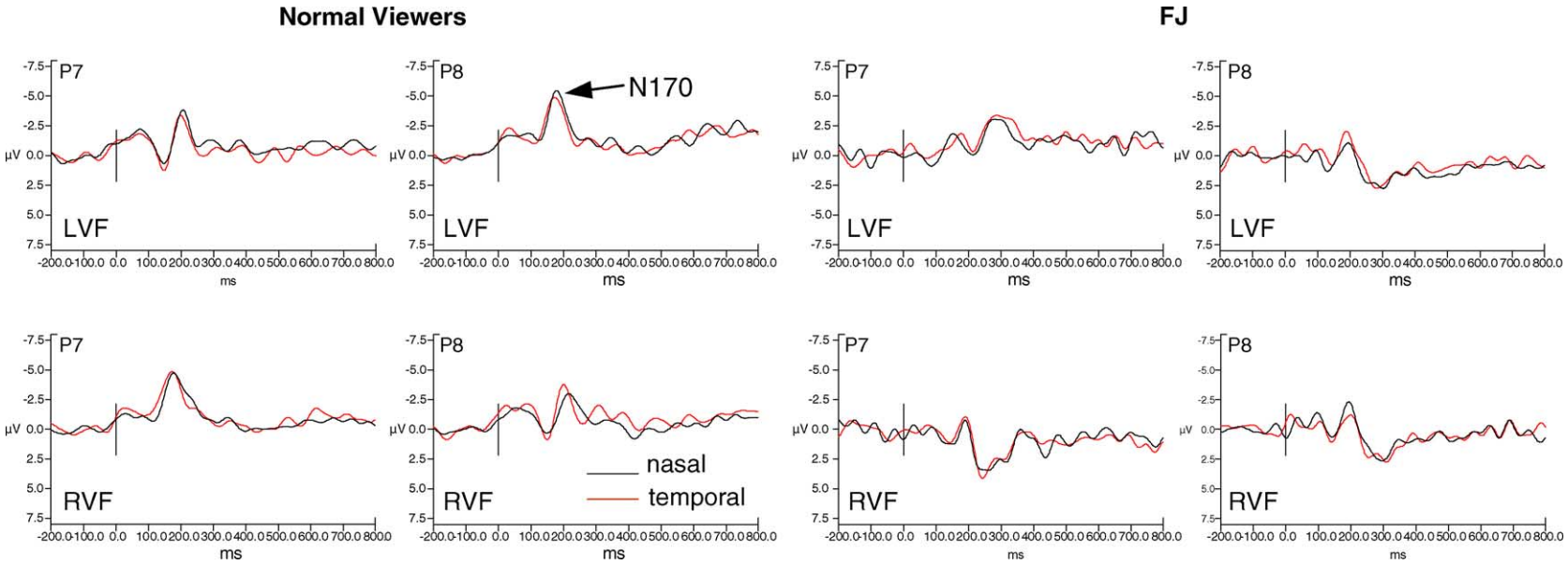

Fig. 2. ERPs of normal viewers and F.J. at electrode positions P7 and P8 to monocularly viewed upright faces presented in the left (LVF) and right (RVF) visual field. Nasal hemiretina ERPs were obtained by presentations to the left eye in LVF and to the right eye in RVF. Temporal hemiretina ERPs were obtained by presentations to the right eye in LVF and to the left eye in RVF.

N170 with higher amplitude for faces presented to the nasal hemiretina. This pattern may be related to preferential orientation to faces previously observed in newborns [22]. The close links between this effect and face processes are underscored by its orientation specificity observed in the LVF. This laterality effect is consistent with many studies indicating preferential processing of whole faces and of configural aspects of the face by the right hemisphere.

Our results suggest that subcortical processing of face stimuli in normal adult viewers may not completely decline after the first months of life. Evidence for an asymmetrical representation of nasal as opposed to temporal retina is well established in retinotectal pathways of mammals but only suggested in humans by fragmentary evidence. Normally it appears that the retinogeniculate pathway so dominates visual processing in primates that any contribution from the tectal pathway is swamped in any but unusual circumstances. In arguing against such a decline our results are consistent with previous studies also indicating that the subcortical route is available in normal adults where inhibition of return (IOR) was investigated [11]. Our study adds to those findings the notion that within this rapid orientation network a certain degree of face specificity may exist. Thus, we provide the missing link between infant abilities and residual visual abilities in patients with complete unilateral loss of striate cortex who nevertheless reliably process faces. At present we speculate that the extra-LGN route encompasses a network of processing structures consisting of superior colliculus, pulvinar, connections to amygdala and also to cortical areas known to be involved in face processing. Further research is needed to understand to what extent a rapid processing route involving amygdala, thalamus, and superior colliculus mediates not only rapid orienting, but also orienting to species-specific information.

Finally, our findings raise an interesting possibility for understanding developmental prosopagnosia. As F.J. shows a deficit in processing faces not only presented centrally, but also presented in the periphery, this might point to a deficit in orienting to faces in F.J. One might speculate that in the developmental framework proposed by Johnson and co-workers, a deficit in the neonatal face system means that there was no preferential orienting to faces of conspecifics in early infancy. As a consequence of this failure normal acquisition of face recognition may be interrupted. Only a few cases of developmental prosopagnosics have been reported in detail in the literature. They may be different either qualitatively, quantitatively or both. For example, F.J. is more severely impaired than, for example, patient Y.T. [2]. In a behavioural study of F.J. using facial expressions there was also no evidence for a preferential processing of facial expressions in the temporal hemifield (unpublished data). One may speculate that some cases of developmental prosopagnosia are related to a deficit in the early stages of face processing as revealed by unattended face processing. This may be related to the early orienting system as indicated here. Others types of developmental prosopagnosia may be more related to deficits in the cortically based face learning system in inferotemporal cortex. This difference may reflect two types of developmental prosopagnosia, possibly amounting to a difference between developmental (or failure to develop a face recognition system) and congenital prosopagnosia (or inability to selectively orient to faces). On this picture, the two face routes—each able to process faces—would coexist [8], rather than the situation envisaged so far where the neonatal one disappears [5,14]. Possibly, in neurologically intact adults the subcortical route is still functional but is inhibited in normal viewing circumstances by the dominant cortical face recognition system. Recent evidence obtained with neurologically intact adults points in the same direction [20].

To conclude, the three main contributions of this study are that (1) we provide evidence that faces presented in the periphery and viewed monocularly still evoke a reliable N170; (2) we provide data indicating that a subcortically based mechanism for detection and orientation to face stimuli might continue to be functional in normal adult viewers rather than declining rapidly after cortical maturation and (3) this mechanism may be absent in developmental prosopagnosia and this may contribute a deficit in acquiring normal face recognition by not providing the brain with input into the face learning system.

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